Influence of niche characteristics and forest type on fern species richness, abundance and plant size along an elevational gradient in Costa Rica

Kluge, J ; Kessler, M

Abstract: An analysis of the fern vegetation on 156 plots along an elevational gradient (45-3400 m) in undisturbed forests in Costa Rica, Central America, showed a hump-shaped pattern of species richness with a maximum of up to 68 species per 400 m² at mid-elevations. This study documents the contribution of specific habitats (forest types: ridges, ravines) and niches within them (dead wood, rocks, growth zones in trees) to the local fern richness and the relation of species richness to elevation and climatic variables. Forests along ravines showed significantly higher species richness, presumably caused by high environmental humidity. The mean number of individuals of occupied niches per species increased significantly with elevation, suggesting that the niche breadth of species increased and that the differentiation of niches decreased with elevation. Both findings may explain the reduced fern species richness towards and above the upper treeline, but not at low elevations. The key factors for the decreases of species richness at the extremes of the gradient are likely to involve climatic conditions.

DOI: https://doi.org/10.1007/s11258-010-9891-x

Originally published at:
Kluge, J; Kessler, M (2011). Influence of niche characteristics and forest type on fern species richness, abundance and plant size along an elevational gradient in Costa Rica. Plant Ecology, 212(7):1109-1121.
DOI: https://doi.org/10.1007/s11258-010-9891-x

Plant Ecol (2011) 212:1109–1121
DOI 10.1007/s11258-010-9891-x

Influence of niche characteristics and forest type on fern species richness, abundance and plant size along an elevational gradient in Costa Rica

Jürgen Kluge · Michael Kessler

Received: 10 June 2010 / Accepted: 21 December 2010 / Published online: 18 January 2011

Abstract An analysis of the fern vegetation on 156 plots along an elevational gradient (45-3400 m) in undisturbed forests in Costa Rica, Central America, showed a hump-shaped pattern of species richness with a maximum of up to 68 species per 400 m^2 at mid-elevations. This study documents the contribution of specific habitats (forest types: ridges, ravines) and niches within them (dead wood, rocks, growth zones in trees) to the local fern richness and the relation of species richness to elevation and climatic variables. Forests along ravines showed significantly higher species richness, presumably caused by high environmental humidity. The mean number of individuals of occupied niches per species increased significantly with elevation, suggesting that the niche breadth of species increased and that the differentiation of niches decreased with elevation. Both findings may explain the reduced fern species richness towards and above the upper treeline, but not at low elevations. The key factors for the decreases of species richness at the extremes of the gradient are likely to involve climatic conditions.

Keywords Climatic environment · Elevational gradient · Ferns · Habitat type · Niche segregation · Tropical forest

Electronic supplementary material The online version of this article (doi:10.1007/s11258-010-9891-x) contains supplementary material, which is available to authorized users.

J. Kluge (✉) · M. Kessler
Systematic Botany, University of Zürich, Zollikerstrasse 107, 8008 Zürich, Switzerland
e-mail: klugejuergen@gmx.de

J. Kluge
Faculty of Geography, University of Marburg, Deutschhausstrasse 10, 35032 Marburg, Germany

Introduction

One of the classical hypotheses used to explain the high tropical plant species richness is niche segregation between species (Willig et al. 2003). The underlying hypothesis is that the less stressful tropical conditions allow a finer niche partitioning relative to temperate zones (Evans et al. 2005). For example, it has been claimed that the wider latitudinal amplitude of species in extratropical regions is a result of adaptations to highly seasonal climates, forcing the species to adapt to a wide range of climatic conditions and thereby enabling them to survive across a wide latitudinal range (Stevens 1989).

The majority of studies on niche segregation among tropical plants have focused on trees (e.g. Lieberman et al. 1996; Losos and Leigh 2004), however, understorey herbs and epiphytes are gaining increasing attention (e.g. Engelbrecht et al. 2000; Jones et al. 2008; Zotz and Hietz 2001). Among trees, some broad guilds can be distinguished with respect to soil nutrient availability and forest structure (e.g. pioneer vs. late-successional species) (Hubbell and

Foster 1990; Hubbell et al. 1999). Similarly, for terrestrial herbs in lowland tropical forests, species distributions can to a large degree be explained by edaphic conditions (e.g. Ruokolainen et al. 1997; Tuomisto et al. 2002, 2003). For epiphytes, microhabitat specialization with respect to tree topography and host tree specificity has been found to be related to taxonomic and physiological traits (Freiberg and Freiberg 2000; Hietz and Hietz-Seifert 1995a; Ingram et al. 1996; Kreft et al. 2004; Zotz and Hietz 2001). In combination, all these studies have documented some major ecological guilds among the study organisms. However, the total number of species is usually much higher than the number of recognizable guilds, and species richness within the guilds cannot be explained by this approach (Hubbell 2001). Partly, this may be due to inability of the observers to perceive existing differences. However, the major drawback in assessing the importance of niche segregation in determining tropical species richness is that very few studies have compared the degree of niche partitioning among tropical and extratropical plant communities. This is certainly due in part to the difficulty of meaningfully comparing communities with often strikingly different taxonomic composition, overall species richness, environmental conditions and historical development. One possible approach to this would be to compare niche segregation along gradients of elevation, where species richness also varies strongly, but where other factors such as biogeographic and historical backgrounds are more similar. This has been attempted in very few studies (e.g. Heaney 2001; Vasquez and Givnish 1998).

In this study, we used a standardized sampling design to survey the fern assemblages in 156 plots along a full elevational gradient of 3300 m in Costa Rica. We conducted microclimatic measurements (temperature and relative air humidity) at four different elevations to examine how microclimate varies along the elevational gradient, between forest types, and along height gradients within single trees. We asked whether different forest types (zonal forest, forests along ravines and ridges) and microclimatic zones within trees influence fern richness, and if these influences vary with elevation.

Ferns and lycophytes (in the following called ferns) are particularly useful groups for this type of study because they are widespread, have a reasonably high but manageable species richness, are of a fairly stable species-level taxonomy, and have an outstanding contribution to local tropical floras inhabiting a wide variety substrates from hot and dry to cold and wet environments (Kappelle and Gomez 1992; Pearson 1995; Ruokolainen et al. 1997).

Materials and methods

Study areas

The elevational gradient studied was composed of two subtransects. Braulio Carrillo National Park and adjacent Biological Station La Selva are located on the Atlantic slopes of Volcán Barva within the Central Volcanic Cordillera of Costa Rica between 45 and 2906 m (Appendix 1 in Supplementary material). This is the most extensive protected elevational gradient of primary tropical forests in Central America (Herrera-McBryde 1997; Pringle et al. 1984).

Because the Volván Barva subtransect does not reach the upper timberline, additional investigations were carried out on the mountain complex of Cerro de la Muerte between 2700 and 3400 m with a timberline at 3200 m and páramo vegetation higher up. Previous analysis of floristic discontinuities along the whole gradient revealed significant species turnover values at 1000 and 3200 m. However, where both subtransects were combined (at 2700–2800 m), such floristic discontinuities could not be observed (Kluge et al. 2008).

Microclimatic measurements

Temperatures and relative air humidity were measured at several locations within four different elevational steps from July 2002 to November 2003 using Microdaq data-loggers HoboPro. At each single location we established a set of three data-loggers at 50 and 200 cm above the ground and on high trunk/in the inner canopy at about 15–20 m. The sites were on the Brava subtransect at 40 m (in zonal forest), at 650 and 1800 m (in zonal, ravine and ridge forests), 2800 m (in zonal and ridge forests). Measurement intervals were 10 min, data were averaged afterwards to 1 h to eliminate possible outliers.

For the present analyses, we used the averaged data of all loggers to characterize the climatic situation in the given elevational belt. Deviations from values of the zonal forest stands to values at

ravine and ridge forest stands, and from every value at 200 cm towards the corresponding value of the same location at 50 cm and in the inner canopy are given to illustrate the different variabilities between and within the forest stands at each elevational step. We used the daily minimum air humidity values, as many ferns are poikilohydric organisms, and lack of water (drought events) are more likely to reflect limiting growing conditions.

As bryophyte cover on trunks and branches is supposed to reflect air humidity in tropical mountains (Frahm and Gradstein 1991), we estimated the bryophyte cover on every plot to validate the measured patterns of air humidity.

Fern vegetation sampling

At 33 regular elevational intervals of 100 m between 100 and 3400 m a.s.l. we established four to five plots to study fern distribution patterns within a field period of 18 months (May 2002–December 2003). Plot area was kept constant to control for sampling effort and area (Lomolino 2001). The size of the square plots was 400 m^2, and all plots were at least 200-m apart. At each elevational step, three plots (zonal forest stands) were randomly placed while avoiding special structural and geomorphological features (e.g. gaps, cliffs, steep valleys). Wherever possible, one or two additional plots were situated in special habitats: one along ravines with permanently running water and steep flanks (at 29 elevational steps), and one on exposed ridges (at 28 elevational steps). Missing plots in special habitats are all above 2800 m and due to lack of suitable sites, either there was no ravine or no marked ridge situation. The plot size is small enough to keep environmental factors and forest structure homogeneous within the plots and is the minimum area required for representative fern surveys (Kessler and Bach 1999).

All fern species were recorded with additional data concerning the numbers of individuals for each species. Vining species (e.g. *Oleandra*) and species with small creeping, interwoven rhizomes (e.g. *Hymenophyllum*) are difficult to count as individuals without destroying whole carpets, and so we treated them as one individual at, e.g. a single tree or branch. All species were noted for their occupied substrates. Terrestrial species were separated into species on normal soil, dead wood and open rocks. Dead wood was any fallen branch or log in advanced state of decay, i.e. of softer texture, with removed bark and/or apparently changed vegetation cover (e.g. with tree fern saplings), as long as its original form was more or less discernible. Records on (recently) fallen branches or logs of intact structure were listed as epiphytes (see below). Open rocks were only found along ravines, where running water or temporal floods avoid accumulation of soil. Rhizomes fixed in soil on parts of rocks protected from running water were treated as normal terrestrials on soil. Hemiepiphytic species (i.e. species rooting in soil, but maintaining lifecycle as epiphytes by climbing) were treated as epiphytes.

Epiphyte sampling was conducted from the ground by climbing lower portions of trunks, the use of collecting poles up to ca. 8–10 m, intensive searches for recently fallen branches in the plots, and visual assessments with binoculars. All epiphytes were separated into low trunk epiphytes (<2 m), high trunk epiphytes (>2 m) and canopy epiphytes. Canopy epiphytes were separated for inner, middle and outer canopy zones following Johansson (1974) by estimating the original position of the fallen branches and observations from the ground.

All species on each plot were noted with an estimated mean of leaf length to account for their general plant size, i.e. taking the length of typical leaves apart from young and exceptional large ones.

Data analysis

The basic measure for species richness was the mean species number of all plots at one elevational step (i.e. mean number of all species, epiphytes or terrestrials in all plots, zonal plots or ravine plots per elevational step). To account for differences of species richness between lifeforms at different scales, we applied *t* tests for matched pairs. To account for the contribution of special forest types (forests along ravines and ridges) to the whole species richness, we ran linear models with forest types as covariate (ANCOVA) to test whether forest types show different elevational richness patterns. Linear regressions were applied to test for any trend of a feature along the elevational gradient.

Where appropriate, analyses were examined for basic lifeforms ('terrestrials', 'epiphytes') separately. Since the special terrestrial substrates 'rock' and 'dead wood' were unfortunately very unevenly represented in the sampling plots, we refrain from

analysing elevational trends for them separately, but treated them as normal terrestrials. Only analyses treating the species set as a whole distinguish between these special substrates.

Results

Microclimate

Mean temperature in zonal forests decreased monotonically with elevation (Fig. 1a, b), with an elevational lapse of ca. 0.56°C × 100 m^{-1}. The temporal variability of temperature in zonal forests was more or less constant with elevation. Within each elevational band, we measured the lowest variation of temperature between forest types at 650 m (Fig. 1c), but the variability between elevations was very low. Comparing the internal forest height gradient at single locations, the variation of temperature was lowest at 1800 m (Fig. 1d), but again the variability was very low.

Minimum relative air humidity (Fig. 2b) increased with elevation up to 1800 m and decreased again towards higher elevations, as reflected by the variability of daily minimum values (amount of dry spells, Fig. 2a) that was lowest at 1800 m. The mean bryophyte cover at every elevational step showed the same humped pattern and was closely correlated to measured air humidity ($R = 0.84$, $P < 0.001$). Within each elevational band, minimum air humidity decreased from ravine to zonal forests to ridges, with the lowest deviations from zonal values in 1800 m and least variability along ravines (Fig. 2c). Again, bryophyte cover mirrored the measured patterns, and along the elevational gradient at each elevational step bryophyte cover was highest along ravines and lowest along ridges, and the differences were significant (ANCOVA, $F = 8.70$, $P < 0.001$). Along the height gradient of single trees, humidity decreased from 50 cm above ground to inner crown (Fig. 1d). This pattern was least pronounced at 1800 m, and the least variability was measured at 50 cm above ground within the same elevation. Analysing microclimate in

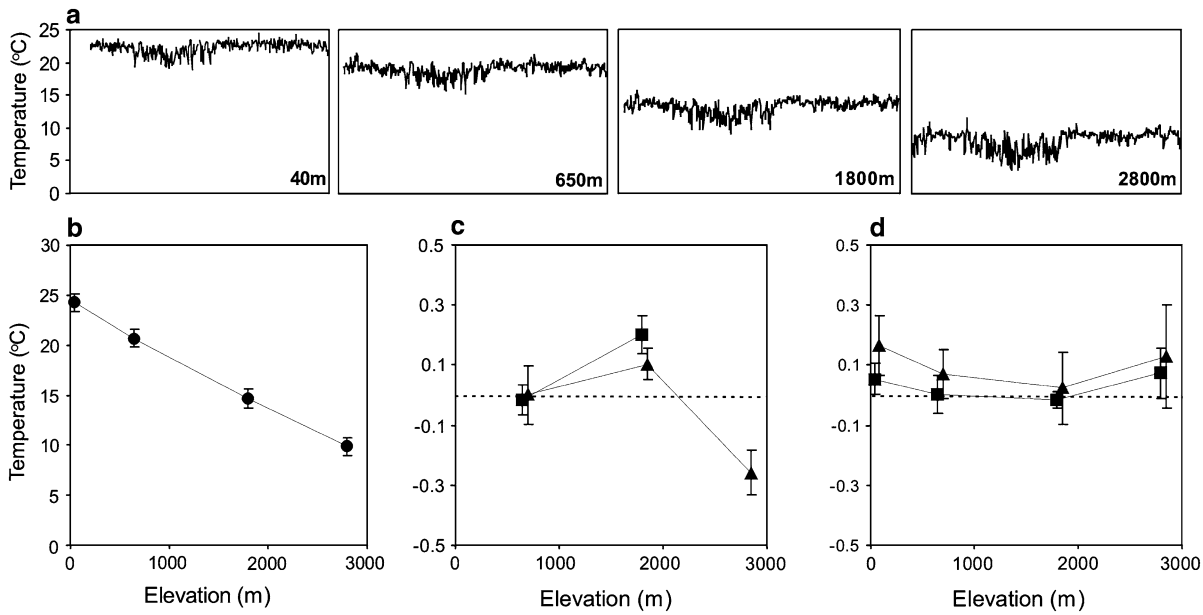


Fig. 1 Temperature data at four elevations along the study transect for the observation period August 2002–December 2003. **a** Daily temperature (means of hourly values) within observation period, calculated from the means of all data loggers at 40, 650, 1800, and 2800 m. **b** Elevational decline of mean temperature during the observation period calculated from the daily means. **c** Mean differences between temperature in ravines (*squares*) and on ridges (*triangles*) relative to temperatures in zonal forest stands. **d** Mean deviation of temperature at 50 cm above ground (*squares*) and in the inner canopy (*triangles*) relative to the temperature at 200 cm at the same location. For clarity of presentation, in **c**, **d** temperature deviations marked with triangles were transferred to the left by 50 m on the elevational scale. Note different scalings of *y*-axis. *Error bars* indicate standard deviations of all day-by-day-means

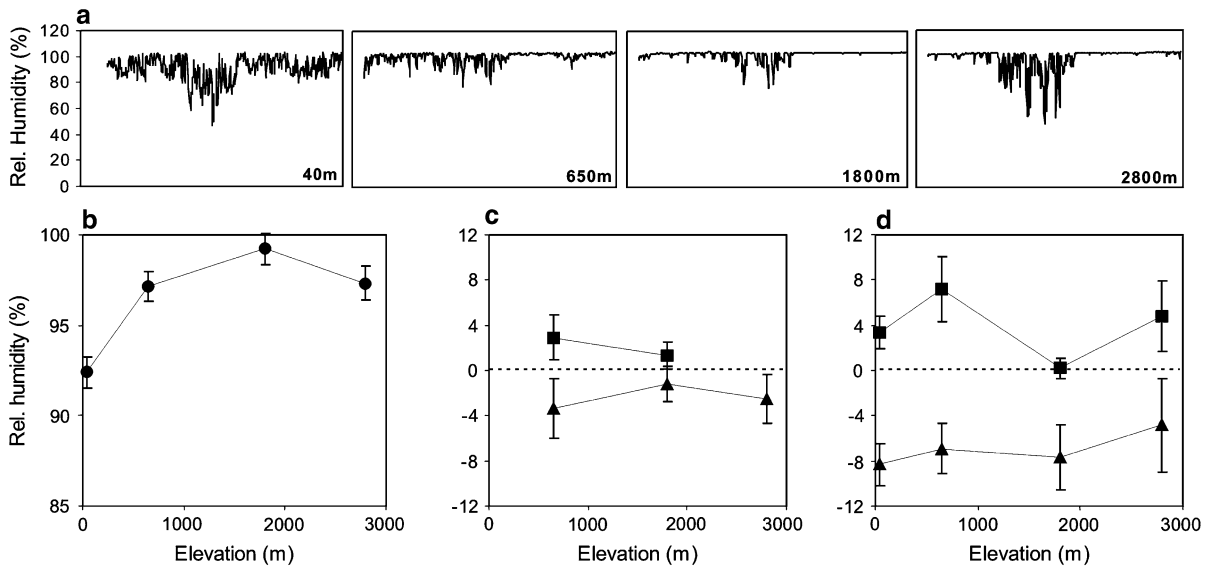


Fig. 2 Relative air humidity at four elevations along the study transect for the observation period August 2002–December 2003. **a** Daily minimum air humidity within observation period, calculated from the means of all data loggers at 40, 650, 1800, and 2800 m. **b** Elevational trend of mean minimum air humidity during the observation period in zonal forests at 200 cm above ground, calculated from the daily means. **c** Mean deviations of minimum air humidity in ravines (*squares*) and on ridges (*triangles*) relative to minimum air humidity in zonal forest stands. **d** Mean deviation of minimum air humidity in 50 cm above ground (*squares*) and in the inner canopy (*triangles*) relative to minimum air humidity in 200 cm at the same location. Note different scalings of *y*-axis. *Error bars* indicate standard deviations of all day-by-day-means

context, we found the most balanced climatic situation regarding temperature and air humidity at mid elevations around 1800 m, in ravine forests, and close to ground level.

Fern assemblages

Within the 156 study plots, spanning an elevational range of 3300 m, we recorded a total of 484 fern species, belonging to 77 genera and 23 families (see full species list given in Appendix 2 in Supplementary material). 78 species (16%) were found in just one plot, and 62 species (13%) in only two plots. Only 52 species (10%) were recorded in more than 15 (i.e. 10%) of the study plots, and only 3 species were found over nearly the entire transect. No less than 194 (40.1%) of the species were found at least once both as terrestrials and epiphytes, while 148 (30.6%) were recorded exclusively as terrestrials and 142 (29.3%) as epiphytes. As a result, including double-notations with respect to life form, we found 342 terrestrial and 336 epiphytic species (Table 1). The ratio of the number of terrestrials to epiphytes per elevational step was scale-dependent, with the mean ratio declining from the whole study area (1.0) to elevational steps (0.8) and to individual plots (0.7).

The percentage of species found at a given elevational band as both terrestrial and epiphytic ranged from 9.8 to 52.2 (mean 24.7%) of the respective species assemblage, with a clear elevational trend of higher proportions towards high elevations ($R^2 = 0.81$, $P < 0.001$; Fig. 3). Of the 194 double-noted species, 146 were mainly epiphytes, but only 48 mainly terrestrials (Table 2). Unsurprisingly, dead wood was the most important terrestrial substrate for epiphytes, and trunks below 2 m the most important epiphytic substrate for terrestrial species, with decreasing importance along the height gradient towards the outer canopy, where no terrestrial species was found.

Along the elevational transect, the number of species showed a clear hump-shaped pattern with highest richness at mid elevations around 1700 m (Fig. 4a). Separated for the major life forms (terrestrials and epiphytes, Fig. 4a), the same pattern emerged, but the hump was more pronounced for epiphytes. Separating the two major life forms for elevational patterns in the three forest types (Fig. 4b–d), epiphytes

Table 1 Ratios of species richness values and mean elevational ranges (standard errors in parentheses) compared for terrestrials and epiphytes

Scale	Terrestrials	Epiphytes	Ratio	*t* test
Total species number	342	336	1.0	
Mean species number per elevational step ($N = 33$)	46.8 (±5.5)	57.9 (±9.9)	0.8	$T = 4.4$
(Min–max)	(19–67)	(8–89)		$P < 0.001$
Mean species number per plot ($N = 156$)	18.9 (±3.4)	28.5 (±5.5)	0.7	$T = 11.5$
(Min–max)	(6–41)	(1–49)		$P < 0.001$
Mean elevational range (m)	636 (±344)	783 (±368)	0.8	$T = 2.7$
(Min–max)	(0–3000)	(0–3100)		$P = 0.007$

A paired *t* test was applied to test for differences between means of terrestrial and epiphytic species

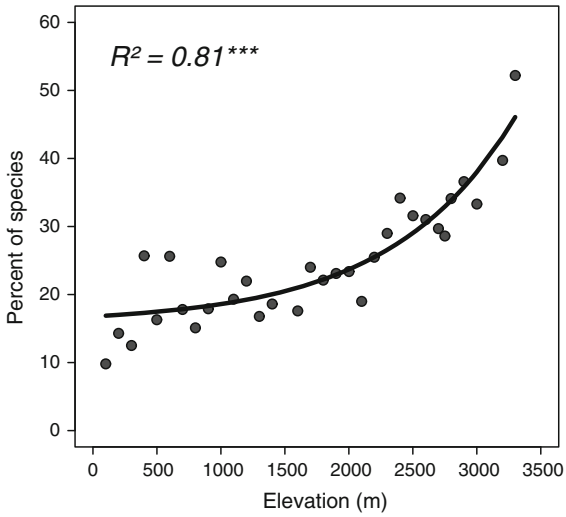


Fig. 3 Proportion of species with double-notations (recorded both as terrestrials and epiphytes) in each elevational belt of 100 m along the elevational gradient. The linear regression with second-order polynomial shows that the increase of species number with double-notations with elevation was significant (***$P < 0.001$)

showed nearly no differences of species richness and elevational lapse of species richness between zonal, ravine and ridge forests (Fig. 4d). Only below 500 m did the number of species along ravines exceed the number of species in the other two forest types. Number and elevational lapse of terrestrial species in zonal and ridge forests were also very similar, but along ravines along the whole elevational gradient species numbers were much higher (up to 2-fold) than in zonal and ridge forests (Fig. 4c; ANOVA, $F = 32.9$, $P < 0.001$). These differences between lifeforms were confirmed by ANCOVA results (Table 3): elevation always gained significance within the quadratic models, habitat type as covariate only revealed significant differences for terrestrial species.

As expected, for epiphytic lifeforms (Fig. 4e–j), in the majority of cases the number of species maintained their patterns with a hump at mid elevations, but some slight differences relative to the coarser life form scale emerged. Trunk and canopy species as a whole followed the prevailing elevational trend with highest species numbers at mid elevations (Fig. 4e–g). The canopy pattern was predominantly caused by species in the middle canopy (Fig. 4i), whereas the inner and outer canopy not only housed a lower number of species but also without such a clear humped elevational trend (Fig. 4h, j). As a result, terrestrial and epiphytic species showed different prevailing deviations from the overall elevational richness pattern of all species: for terrestrial species it was the differences between forest types, and for epiphytes it was the height gradient along the host trees.

The number of occupied substrates (microhabitats, niches) of epiphytes was positively correlated with elevation (Fig. 5a), i.e. species assemblages at low elevations showed on average a higher degree of segregation between microhabitats than species assemblages at high elevations.

The mean number of individuals per plot showed a humped pattern along the elevational gradient with maximum number of individuals between about 1800 and 2500 m (Fig. 5b). In contrast, the mean number of individuals per species had a monotonic increase with elevation with highest values towards upper tree line (Fig. 5c). The mean size of species per plot showed a humped pattern with highest values at mid elevations and a sharper decrease towards high elevations (Fig. 5d).

Table 2 Number of species found as both life forms, terrestrials and epiphytes (double-noted species), and number (*N*) and percentage number (%) of species found as well as in the respective other habitats

Double-noted species (total number)	Found as well in these terrestrial habitats	*N*	%
Epiphytes ($N = 146$)	Soil	75	51.4
	Dead wood	130	89.0
	Open rocks	28	19.2
Double-noted species (total number)	Found as well in these epiphytic habitats	*N*	%
Terrestrials ($N = 48$)	Trunks < 2 m	47	97.9
	Trunks > 2 m	15	31.3
	Inner canopy	4	8.3
	Middle canopy	2	4.2
	Outer canopy	0	0

Discussion

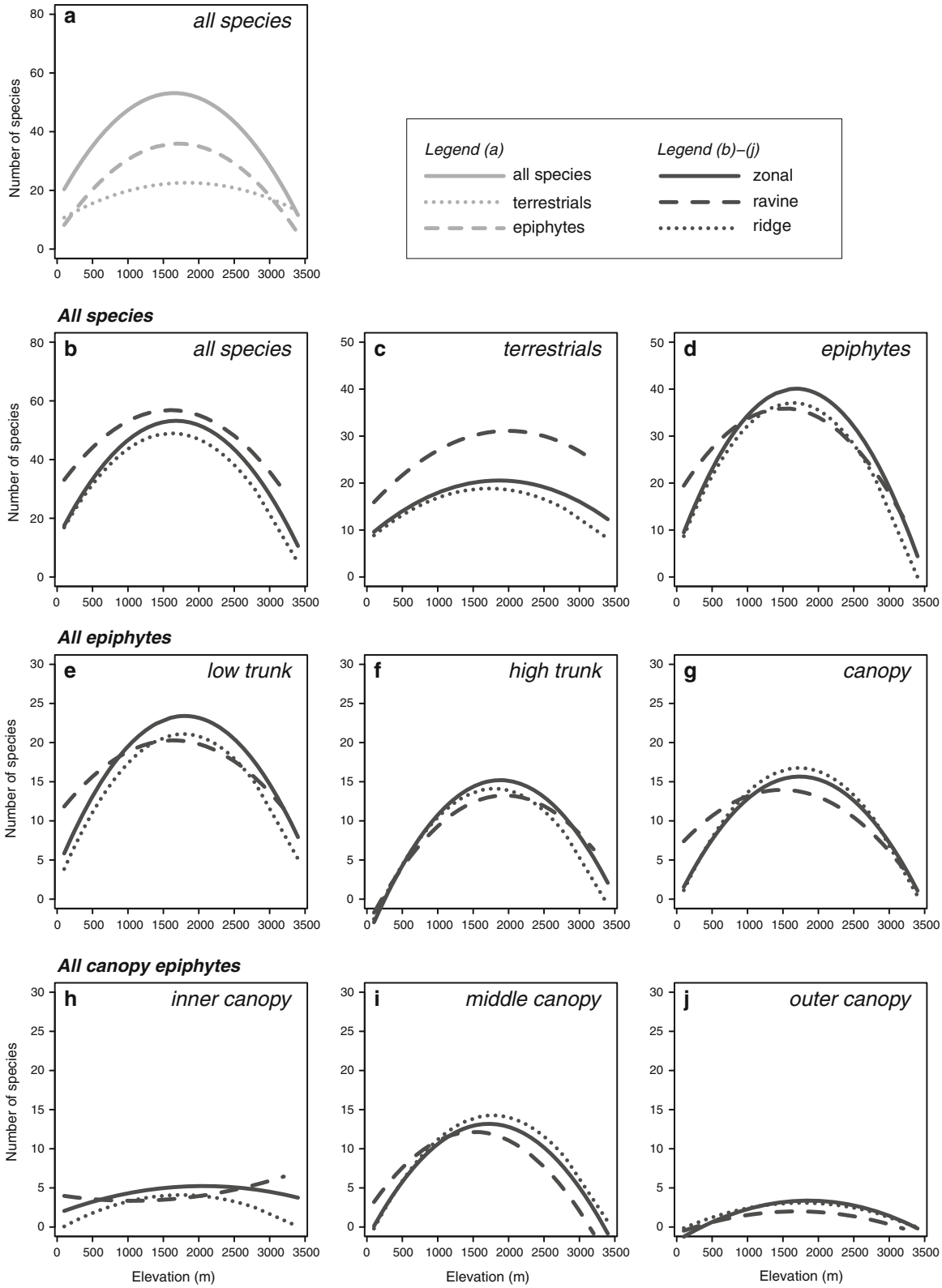
With this study we document the contribution of special habitats and/or substrates to the local fern richness in a tropical montane ecosystem, including measurements of relevant microclimatic factors (temperature and air humidity), and to compare the revealed patterns along an elevational gradient. The mid-elevational hump of species richness found in this study corresponds to the common pattern within the tropics for many plant groups (e.g. Bhattarai and Vetaas 2003; Hemp 2002; Kessler 2001; Watkins et al. 2006) and possible mechanisms involved are discussed elsewhere (Kluge et al. 2006). Our discussion here will focus on the (a) contribution of different habitats and niches to overall fern species richness and (b) question whether niche breadth of the species increases with elevation and if this can account for reduced richness at high elevations.

Habitat and niche diversity

The separation by forest types shows that topographically determined habitat types were partly inhabited by distinct fern assemblages. Terrestrial species were far more species-rich along ravines than in adjacent zonal forests, with up to twice as many species, showing the importance of this habitat for overall fern species richness. This is most likely due to the constantly high local air and soil humidity in the proximity of streams and the availability of special habitats such as exposed earth banks (Tuomisto and Ruokolainen 1994). Species richness along ridge habitats proved to be lower compared to adjacent zonal habitats, but since on average less than 10% of the terrestrial species were restricted to this habitat, the differences were not significant. A similar low number of fern species on ridges has also been found in Ecuador (Kessler and Lehnert 2009). This suggests that ridge habitats are of limited importance for enhancing regional fern diversity.

In contrast to the terrestrial species, for epiphytes we did not find any evidence that forest types might have an influence on species richness patterns along the elevational gradient. This is surprising, as air humidity is one of the major driving factors for epiphytic richness (Kluge et al. 2006; Krömer et al. 2005; Cardelus et al. 2006). However, especially at higher altitudes along the host tree gradient from tree base to outer canopy, 'cloud stripping' by host trees (i.e. harvesting additional water surplus from clouds rolling by) may compensate topography-driven high humidity at valley bottoms.

Embedded in this rough structure of forest types, the further differentiation of the epiphytic niches along host tree gradients arranges the spatial distribution of richness patterns on a finer scale, and offer insight into the structure of microhabitat characteristics and the contribution of different niches to overall species richness. Canopy epiphytes generally showed highest species richness in the middle canopy and lower richness in the inner and outer canopy. Both of these latter niches are, for different reasons, less favourable sites for fern growth. The outer canopy has the most extreme climatic conditions with a high variation in temperature and air humidity, causing dry and/or cold events (Hietz and Hietz-Seifert 1995b). Furthermore, small branches and twigs in the outer canopy limit


a
all species
Number of species
Legend (a)
all species
terrestrials
epiphytes
Legend (b)–(j)
zonal
ravine
ridge
All species
b
all species
c
terrestrials
d
epiphytes
All epiphytes
e
low trunk
f
high trunk
g
canopy
All canopy epiphytes
h
inner canopy
i
middle canopy
j
outer canopy
Elevation (m)

◀ **Fig. 4** Species richness along the elevational gradient from 100 m to 3400 m. **a** Richness of all species (*continuous line*), terrestrials (*short-dashed line*) and epiphytes (*long-dashed line*). **b–j** Richness within all following figures separated by forest types: zonal forest (*continuous lines*), ravine forest (*long-dashed lines*), and ridge forest (*short-dashed lines*). **b–d** Richness of all species and major life forms (terrestrials and epiphytes). **e–g** Richness of major epiphytic habitats. **h–j** Richness of canopy substrates. For clarity of presentation, only trendlines are given

Table 3 ANCOVA; linear models of species richness of different lifeforms against elevation (including quadratic term) always reached significant results ($P < 0.05$)

Life form	ANCOVA			Post hoc (Tukey)		
	R^2	F	P	Zonal	Ravine	Ridge
Terrestrials	0.64	38.25	<0.001	a	b	a
Epiphytes	0.71	102.90	<0.001	a	a	a
Low trunk	0.47	39.10	<0.001	a	a	a
High trunk	0.60	65.91	<0.001	a	a	a
All canopy	0.51	14.13	<0.001	a	a	a
Inner canopy	0.23	2.99	0.006	a	a	a
Middle canopy	0.59	19.70	<0.001	a	a	a
Outer canopy	0.21	12.08	<0.001	a	a	a

Including habitat types (zonal, ravine and ridge) as covariate was only significant for terrestrial as indicated by Tukey post hoc test (different letters *a*, *b* indicate significant differences between habitat types)

substrate accumulation, confining this niche to highly adapted specialists (Bøgh 1992). Consequently, physiological traits of these species (e.g. leaf thickness, stomatal density, desiccation rate) correlate with degree of exposure of the epiphytes (Hietz and Briones 1998). The inner canopy has, compared to the outer canopy, more favourable abiotic growing conditions (Freiberg and Freiberg 2000) with higher accumulations of soil in branch forks and more balanced climatic conditions, but there is high competition with other epiphytic plant groups such as orchids, Araceae and Ericaceae that often have sub-shrubby stature, leaving less space for the usually small-sized epiphytic ferns (see also Benzing 1987; ter Steege and Cornelissen 1989).

Transition between niches

Beyond these findings of species richness patterns with respect to habitat and niche differentiation, the terrestrial and epiphytic life forms are not strictly separated spheres, and transitions between both life forms provides further insights about the structural similarities between habitats. We found an approximately even number of terrestrials and epiphytes regarding the whole species set (342 terrestrials vs. 336 epiphytes). Since total species number was 484 species, the list includes a high fraction of double-noted species, i.e. species that normally occurred as terrestrials, but occasionally as well as epiphytes, and vice versa ($N = 194$, Table 2). This distinction is necessarily subjective to a certain degree. Whether an epiphytic that has fallen to the ground is still called an epiphyte or rather now terrestrial, is a matter of conjecture. We treated recently fallen plants as epiphytes and only those as terrestrial plants which had obviously survived for a longer time period and was actively growing in its new habitat. Moreover, the selection of such accidental epiphytic or terrestrial plants is not stable through time. We observed a certain fraction of double-noted species, and while at another point in time there would likely be a similar number of such observations, these would probably include a different set of species. Despite these uncertainties, there were a number of clear patterns.

Trunk bases offered the most suitable epiphytic niches for terrestrial ferns, having similar microclimatic conditions as the forest understorey (Krömer et al. 2007; Nieder et al. 1999). The importance of other epiphytic niches for terrestrial species decreased with height above the ground, reflecting the increasingly different microhabitat conditions (amount of soil and soil moisture, see also Parker 1995). Similar results are provided by Watkins et al. (2006) along the same gradient, although they found only one fern species present from ground layer to canopy. Epiphytes, on the other hand, were found outside their epiphytic habitats mostly on dead wood. This is easy to understand, as dead wood is structurally and chemically more similar to living trees than bare soil, and a number of the records presumably refer to epiphytes surviving after tree- and branchfall. Within the list of double-noted species, epiphytes were by far better represented than terrestrials (144 and 48 species, respectively). This may partly be due to the above-mentioned 'epiphyte-rain' within the forest, but is also likely to reflect the different ecological conditions of the epiphytic habitat compared to the terrestrial one (Nadkarni 1988). Although a fallen epiphyte is usually in its final chapter of life (Matelson et al. 1993), it has a higher probability

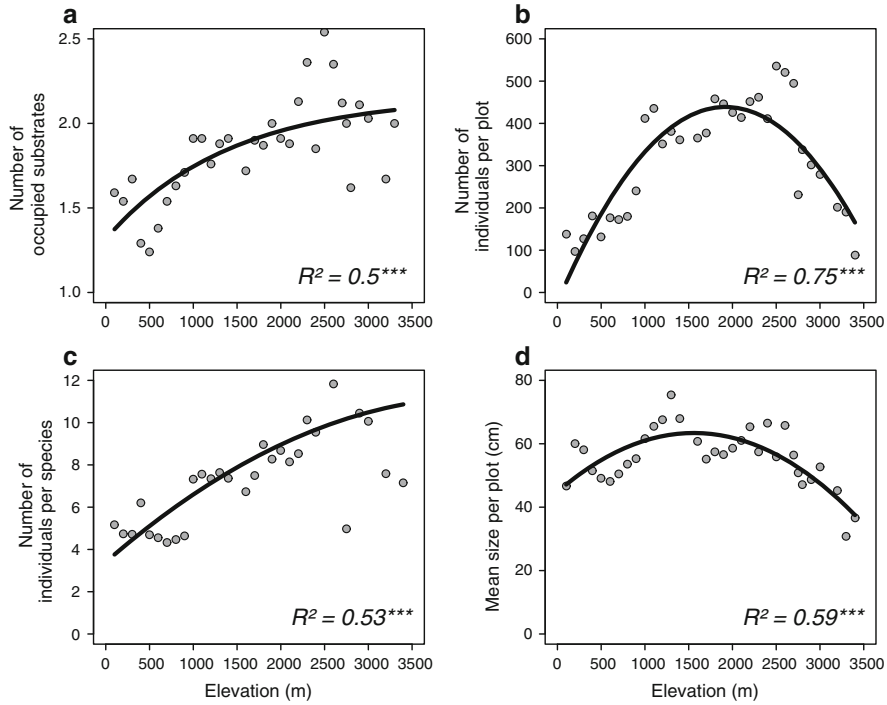


Fig. 5 **a** Mean number of occupied substrates of species assemblages with respect to elevation (only epiphytic species); **b** mean number of individuals per plot at each elevational step of 100 m; **c** mean number of individuals per species at each elevational step of 100 m; **d** mean plant size of species per plot. *** $P < 0.001$

to survive for a while than a terrestrial species that has to occupy an epiphytic niche.

As noted above, terrestrial and epiphytic niches are fundamentally different, and it is apparent that their spatial distribution is different for the terrestrial and epiphytic life forms. Although the species number of both life forms in the whole dataset is balanced, the relation turned into a dominance of epiphytes with decreasing area considered (Table 1), a pattern also found in Bolivia (Kessler 2001; Krömer et al. 2005). This indicates that epiphytic species are more widely and regularly distributed than terrestrials, as also evidenced by the larger mean elevational amplitude of epiphytes. The high local species density of epiphytes appears to be caused by their smaller overall size, higher number of individuals per area, and greater habitat variability in a given plot. A further aspect to consider here is a possible hidden species–area relationship, since the whole surface of trunks and branches within a plot of a given size exceeds the ground-area of the plot. Further, terrestrial species showed a stronger differentiation between major forest types (zonal, ravine and ridge) than epiphytes, which in turn had the most obvious differences relative to position within trees. While different niches for terrestrial plants (e.g. different soil types) are typically found over distances of at least several tens of meters (Tuomisto et al. 2003), i.e. beyond the area covered by a single of our plots, for epiphytes an individual tree spans an entire cosmos of niche differentiation, depending mainly on canopy topography (Krömer and Gradstein 2003) and less on the tree species itself (Hietz and Hietz-Seifert 1995a; Ibisch 1996).

Niche breadth

Overall, niche breadth of the individual species appears to increase along the elevational gradient. This is supported by several observations. First, the mean number of individuals per species increases with elevation (Fig. 5c), indicating that despite overall more extreme and spatially less variable habitat conditions, those fern species that can survive at high elevations achieve higher local abundances. This is not merely a consequence of smaller individual plant sizes, since plant sizes peaked at mid elevations together with overall individual numbers (Fig. 5d). This pattern may be confounded by relative contribution of other plant groups competing for space. However, along our study gradient, Cardélus et al. (2006) found that the proportion of ferns in the

total epiphyte richness strongly increases with elevation, a pattern also found by Krömer et al. (2005) in Bolivia and for terrestrial herbs along and elevational transect in Indonesia (D. Cicuzza, unpublished data) (Fig. 6). This suggests that competition by other herbaceous plants decreases with elevation, which by itself would increase the niche space available to the ferns. Second, the proportion of species recorded both as epiphytes and terrestrials increased with elevation (Fig. 3), a pattern found also by Watkins et al. (2006) along the same gradient with an increasing species overlap between terrestrials and trunk epiphytes. Third, the capability of epiphytic species to grow in different zones on the host tree (trunk and canopy zones) increased with elevation (Fig. 5a).

The latter two patterns could be interpreted to imply either that (a) species tend to have wider niche breadths at high elevations, and/or (b) the differentiation of microhabitats decreases towards high elevations. Most probably, both the factors are involved. At least for the epiphytic realm, it is clear that the differentiation of niches decreases from the tall lowland forest with a closed canopy and a dark understorey to the stunted forest close to timberline,

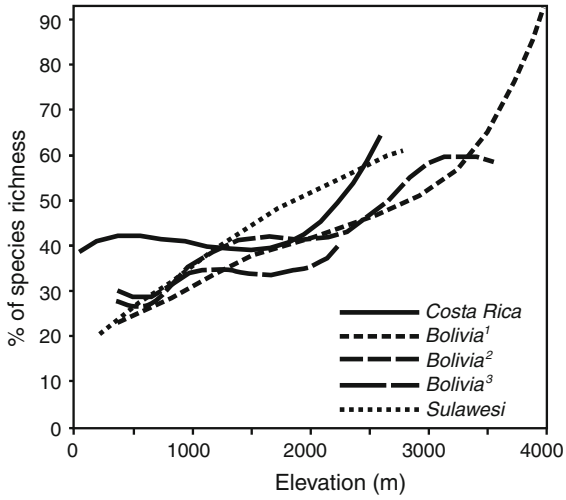


Fig. 6 Relative contribution (%) of ferns to total vascular herbaceous plant species richness along tropical elevational gradients for epiphytes in Costa Rica (*continuous line*, based on data from Cardélus et al. 2006) and Bolivia (*dashed lines*, based on data from Krömer et al. 2005) and for terrestrial herbs in Sulawesi (*dotted line*, based on unpublished data of D. Cicuzza et al.). Subdivisions for Bolivian data: *1* epiphytes on single trees; *2* epiphytes on plots of 400 m^2; *3* epiphytes on plots of 1 ha. For clarity of presentation, only trendlines are shown

which commonly has a relatively open canopy (see 3elle 1996). On the other hand, the increase of the number of individuals per species strongly suggests that niche breadth in fact increases.

Conclusions

The main question of our study was whether the changes of fern species richness along the elevational gradient can be explained by differences in the number of habitats and niches and/or the niche breadth of the species themselves. In this context, it is interesting to contrast the situations at low and high elevations, because both have lower fern richness than mid elevations, but with strikingly different environmental settings.

Patterns in habitat segregation and life form selection support the notion that niche breadth increased at high elevations. This increase was probably not merely due to reduced interspecific competition, because at low elevations, where fern richness was also reduced relative to the richness peak at mid elevations, there was no indication of increased niche breadth among the ferns. Rather, the increase of niche breadth at high elevations may be a result of the more stressful environmental conditions that limit the adaptability of species to narrow niches (Stevens 1992).

Thus, the low fern richness at high elevations may at least be partly due to reduced niche number and wider niche breadth of the species. Whether this increase of niche breadth limits overall fern species richness at these elevations is a different matter. With the data at hand, we cannot determine if the communities are saturated, i.e. if species richness is limited by interspecific competition. This is an essential requirement if larger niche breadth is to reduce overall species richness, otherwise, wider niches would simply lead to increased local richness.

Furthermore, even within specific niches that were comparable at low and mid elevations (e.g. soil, the outermost canopy), species richness was generally lower at high elevations. This indicates that the decline of species richness at high elevations is not only due to reduced niche variability or due to wider niche breadth of the occurring species, but also, and perhaps mainly, due to a different, as yet undisclosed mechanism, most probably involving extreme environmental conditions, especially low temperatures, as also discussed by Hawkins et al. (2003) for a similar

pattern across latitude. A parallel situation is presumably also true for low elevations, where reduced species richness is not correlated with reduced niche number or niche breadth, and where unsuitable environmental conditions, especially periodic water deficit may limit fern richness.

Acknowledgements This study was financially granted by the Deutsche Forschungsgemeinschaft DFG and Deutscher Akademischer Austauschdienst DAAD. We thank Felix Corrales for invaluable help during the field work, the park rangers of the Sistema Nacional de Area de Conservaciones (SINAC) and the Area de Conservación Cordillera Volcánica Central (ACCVC) in Costa Rica, the staff of Biological Station La Selva and the Organization for Tropical Studies OTS, and the National Herbarium in San José for logistical support. For support on identification of fern collections, we thank A. Rojas (*Elaphoglossum*), I. Valdespino (*Selaginella*), B. Øllgaard (*Huperzia*), D. Barrington (*Polystichum*) and A.R. Smith, R.C. Moran and L.D. Gomez in cases of doubt. We thank Pete Reynoldsen and two anonymous reviewers for valuable comments on the manuscript.

References

Benzing D (1987) Vascular epiphytism: taxonomic participation and adaptive diversity. Ann Mo Bot Gard 74:183–204

Bhattarai KR, Vetaas OR (2003) Variation in plant species richness of different life forms along an subtropical elevation gradient in the Himalayas, east Nepal. Glob Ecol Biogeogr 12:327–340

Bøgh A (1992) Composition and distribution of the vascular epiphyte flora of an Ecuadorian rain forest. Selbyana 13:25–34

Cardélus LC, Colwell RK, Watkins JE Jr (2006) Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. J Ecol 95:144–156

Engelbrecht BMJ, Velez V, Tyree MT (2000) Hydraulic conductance of two co-occurring neotropical understory shrubs with different habitat preferences. Ann For Sci 57:201–208

Evans KL, Warren PH, Gaston KJ (2005) Species-energy relationships at the macroecological scale: a review of the mechanisms. Biol Rev 80:1–25

Frahm J-P, Gradstein SR (1991) An altitudinal zonation of tropical rain forests using bryophytes. J Biogeogr 18:669–678

Freiberg M, Freiberg E (2000) Epiphyte diversity and biomass in the canopy of lowland and montane forests in Ecuador. J Trop Ecol 16:673–688

Hawkins BA, Field R, Cornell HV, Currie DJ, Guègan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117

Heaney LR (2001) Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. Glob Ecol Biogeogr 1:15–39

Hemp A (2002) Ecology of the pteridophytes on the southern slopes of Mt. Kilimanjaro I. Altitudinal distribution. Plant Ecol 159:211–239

Herrera-McBryde O (1997) Braulio Carrillo—La Selva Region, Costa Rica. In: Davis SD, Heywood VH, Herrera-Mcbryde O, Villa-Lobos J, Hamilton AC (eds) Centers of Plant Diversity. A Guide and Strategy for their Conservation, vol 3. The Americas. IUCN-Publ. Unit, Cambridge, pp 203–208

Hietz P, Briones O (1998) Correlation between water relations and within-canopy distributions of epiphytic ferns in a Mexican cloud forest. Oecologia 114:305–316

Hietz P, Hietz-Seifert U (1995a) Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. J Veg Sci 6:487–498

Hietz P, Hietz-Seifert U (1995b) Structure and ecology of epiphyte communities of a cloud forest in central Veracruz, Mexico. J Veg Sci 6:719–728

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Monogr Popul Biol 32:1–375

Hubbell SP, Foster RB (1990) Structure, dynamics and equilibrium status of old-growth forest on Barro Colorado island. In: Gentry AH (ed) Four Neotropical Forests. Yale University Press, New Haven, pp 522–541

Hubbell SP, Foster RB, O'Brien ST, Harms KE, Condit R, Wechsler B, Wright SJ, De S Lao L (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. Science 283:554–557

Ibisch LI (1996) Neotropische Epiphytendiversität—das Beispiel Bolivien. Archiv Naturwissenschaftliche Dissertationen, Bd. 1, 357 pp

Ingram SW, Ferrell-Ingram K, Nadkarni NM (1996) Floristic composition of vascular epiphytes in a neotropical cloud forest, Monteverde, Costa Rica. Selbyana 17:88–103

Johansson DR (1974) Ecology of vascular epiphytes in West-African rain forest. Acta Phytogeogr Suecica 59:1–136

Jones MM, Tuomisto H, Borcard D, Legendre P, Clark DB, Olivas PC (2008) Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. Oecologia 155:593–604

Kappelle M (1996) Los Bosques de Roble (Quercus) de la Cordillera de Talamanca, Costa Rica. Instituto Nacional de Biodiversidad: Universidad de Amsterdam, 336 p

Kappelle M, Gomez LD (1992) Distribution and diversity of montane Pteridophytes of the Chirripo national Park, Costa Rica. Brenesia 37:67–77

Kessler M (2001) Patterns of diversity and range size of selected plant groups along an elevational transect in the Bolivian Andes. Biodivers Conserv 10:1897–1921

Kessler M, Bach K (1999) Using indicator groups for vegetation classification in species-rich Neotropical forests. Phytocoenologia 29:485–502

Kessler M, Lehnert M (2009) Do ridge habitats contribute to pteridophyte diversity in tropical montane forests? A case study from southeastern Ecuador. J Plant Res 122: 421–428

Kluge J, Kessler M, Dunn RR (2006) What drives elevational patterns of diversity? A test of geometric constraints, climate, and species pool effects for pteridophytes on an elevational gradient in Costa Rica. Glob Ecol Biogeogr 15:358–371

Kluge J, Bach K, Kessler M (2008) Elevational distribution and zonation of tropical pteridophyte assemblages in Costa Rica. Basic Appl Ecol 9:35–43

Kreft H, Koster N, Kuper W, Nieder J, Barthlott W (2004) Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuni, Ecuador. J Biogeogr 31:1463–1476

Krömer T, Gradstein SR (2003) Species richness of vascular epiphytes in two primary forests and fallows in the Bolivian Andes. Selbyana 24:190–195

Krömer T, Kessler M, Gradstein SR, Acebey A (2005) Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. J Biogeogr 32:1799–1810

Krömer T, Kessler M, Gradstein SR (2007) Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory. Plant Ecol 189:261–278

Lieberman D, Lieberman M, Peralta R, Hartshorn GS (1996) Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. J Ecol 84:137–152

Lomolino MV (2001) Elevation gradients of species-density: historical and prospective views. Glob Ecol Biogeogr 10:3–13

Losos EC, Leigh EG Jr (2004) Tropical forest diversity and dynamism. Findings from a large-scale plot network. The University of Chicago Press, Chicago

Matelson TJ, Nadkarni NM, Longino JT (1993) Survivorship of fallen epiphytes in a neotropical cloud forest, Monteverde, Costa Rica. Ecology 74:265–269

Nadkarni NM (1988) Tropical ecology from a canopy perspective. Mo Calif Acad Sci 12:189–208

Nieder J, Engwald S, Barthlott W (1999) Patterns of neotropical epiphyte diversity. Selbyana 20:66–75

Parker GG (1995) Structure and microclimate of forest canopies. In: Lowman MD, Nadkarni NM (eds) Forest canopies. Academic Press, San Diego, pp 73–106

Pearson DL (1995) Selecting indicator taxa for the quantitative assessment of biodiversity. In: Hawksworth DL (ed) Biodiversity. Measurement and estimation. Chapman and Hall, London, pp 75–80

Pringle CM, Chacon I, Grayum MH, Greene HW, Hartshorn GS, Schatz GE, Stiles FG, Gòmez C, Rodrìguez M (1984) Natural History observations and ecological evaluation of the La Selva Protection Zone, Costa Rica. Brenesia 22:189–206

Ruokolainen K, Linna A, Tuomisto H (1997) Use of Melostomataceae and pteridophytes for revealing phytogeographical patterns in Amazonian rain forests. J Trop Ecol 13:243–256

Stevens GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. Am Nat 133:240–256

Stevens GC (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. Am Nat 140:893–911

Ter Steege H, Cornelissen JHC (1989) Distribution and ecology of vascular epiphytes in lowland rainforest of Guyana. Biotropica 21:331–339

Tuomisto H, Ruokolainen K (1994) Distribution of Pteridophyta and Melostomataceae along an edaphic gradient in an Amazonian rain forest. J Veg Sci 5:25–34

Tuomisto H, Ruokolainen K, Poulsen AD, Moran RC, Quintana C, Cañas G, Celi J (2002) Distribution and Diversity of Pteridophytes and Melastomataceae along Edaphic Gradients in Yasuní National Park, Ecuadorian Amazonia. Biotropica 34:516–533

Tuomisto H, Ruokolainen K, Aguilar M, Sarmiento A (2003) Floristic patterns along a 43-km long transect in an Amazonian rain forest. J Ecol 91:743–756

Vasquez JA, Givnish TJ (1998) Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán. J Ecol 86:999–1020

Watkins JE Jr, Cardelús C, Colwell RK, Moran RC (2006) Species richness and distribution of ferns along an elevational gradient in Costa Rica. Am J Bot 93:73–83

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu Rev Ecol Evol Syst 34:273–309

Zotz G, Hietz P (2001) The physiological ecology of vascular epiphytes: current knowledge, open questions. J Exp Bot 52:2067–2078